

## Cyst morphology of European brachiopods (Crustacea: Anostraca, Notostraca, Spinicaudata, Laevicaudata)

by Alain THIÉRY, Ján BRTEK and Charles GASC

**Abstract.** — A comparative analysis of cyst (= resting egg) size and shell architecture by scanning electron microscopy is reported in 40 species of "large brachiopods", belonging to 21 genera from all the families inhabiting inland waters of Europe. This paper follows one on the geographic distribution of the European brachiopods where 72 species and subspecies belonging to 22 genera and 13 families were listed (BRTEK & THIÉRY, 1995). Particular attention has been paid to cyst shape and morphology of the external shell surface. The results are discussed in the light of existing literature. When the taxonomic value of the external shell surface pattern shows its limits, the combination size/surface pattern seems more useful, being sometimes species-specific, while in other cases (such as in *Branchipus*, *Tanymastix*, *Cyzicus*, *Imnadia*) it appears to reflect taxonomic relationships of higher rank. In other cases, a third character, the structure of the cyst envelope, observable in fractured cysts, must be taken into account to separate cysts (as in *Artemia* sp. and *Branchinectella*). "Large brachiopods" eggs can provide new taxonomic information that is useful in the definition of natural groups.

**Keywords.** — Cyst morphology, resting egg, Europe, Crustacea, Anostraca, Notostraca, Spinicaudata, Laevicaudata, scanning electron microscopy, taxonomy.

### Morphologie des œufs de brachiopodes européens (Crustacea: Anostraca, Notostraca, Spinicaudata, Laevicaudata)

**Résumé.** — La morphologie des œufs (= œufs de résistance) de 40 espèces de brachiopodes (Anostraca, Notostraca, Spinicaudata, Laevicaudata) appartenant à 21 genres représentant toutes les familles peuplant les eaux stagnantes continentales d'Europe, est décrite au moyen du microscope électronique à balayage. Cette étude fait suite à l'article de BRTEK & THIÉRY (1995) qui dresse l'inventaire actuel de ces crustacés brachiopodes en Europe et illustre la distribution géographique des 72 espèces et sous-espèces répertoriées, représentantes de 22 genres et 13 familles. La forme des œufs et la morphologie externe de leur enveloppe sont décrites, les résultats étant confrontés aux données bibliographiques. Dans de nombreux cas, les ornementations de surface sont des critères fiables permettant une identification spécifique ou générique. Lorsque ces ornementations ne présentent pas de caractéristiques suffisantes pour établir une discrimination des œufs, il est alors nécessaire de considérer la combinaison diamètre/ornementations de surface qui peut être spécifique ou parfois générique comme c'est le cas pour les genres *Branchipus*, *Tanymastix*, *Cyzicus* et *Imnadia*. Dans quelques cas, un troisième caractère, la structure interne de l'enveloppe de l'œuf, observable en coupe, doit être considéré pour séparer des œufs d'aspect identique mais d'espèces différentes (cas pour *Artemia* sp. et *Branchinectella media*). La morphologie des œufs de brachiopodes, ayant une incontestable valeur taxonomique, devrait être prise en compte pour compléter les études sur la phylogénie de ces crustacés.

**Mots-clés.** — Morphologie, œufs de résistance, Europe, Crustacea, Anostraca, Notostraca, Spinicaudata, Laevicaudata, microscope électronique à balayage, taxonomie.

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## INTRODUCTION

“Large branchiopods” – fairy shrimps (Anostraca), tadpole shrimps (Notostraca) and clam shrimps (Spinicaudata + Laevicaudata) – are crustaceans living in inland temporary freshwaters, or sometimes saltwaters. As they live in physically and chemically fluctuating astatic habitats, with recurrent phases of complete drying (temporary ponds, ditches, salterns...), these crustaceans present adaptations to desiccation, the main one being the production of only one sort of egg – thick-walled resting eggs (= cysts). The morphology of cysts has been described since the work of DADAY (1910 to 1927) and in several cases specific distinctness has been hypothetized. During the mid- and late 1980s, the micromorphology of cysts has been a central topic in “large branchiopods” biology. Scanning electron microscopy has been used to obtain accurate images of fine surface structures and increasing knowledge has led a number of authors to consider and discuss the taxonomic importance of the micromorphology and size of the cysts (review in THIÉRY & GASC, 1991; De WALSCHE *et al.*, 1991; MURA, 1992a, b). While for several countries cyst morphology has been studied, (Spain: ALONSO & ALCARAZ, 1984, all the orders; Italy: MURA, 1986, 1992a, both only anostracans; France: THIÉRY & GASC, 1991, all the orders), no global view on the European scale is available. The present study is the first one to attempt a synthesis.

## MATERIAL AND METHODS

### IDENTIFICATION

Species identifications were made using adult morphology (second antenna and penes of the male; female ovisac), using DADAY (1910 to 1927), LINDER (1941), BRTEK (1959, 1964, 1966), LONGHURST (1955), STRASKRABA (1965a, b; 1966). Branchiopod taxonomy follows FRYER (1987) and BRTEK & THIÉRY (1995).

The surveyed area is shown in Fig. 1.

### SEM STUDIES

Cysts were removed from female ovisacs, kept in 10% formaldehyde, then fixed in a bath of KAAD (30% kerosene, 60% absolute ethanol, 5% acetic acid, 5% dioxane) for 24 h (see THIÉRY & GASC, 1991). From preserved females, we chose only individuals with well formed complete egg-shells. The egg-shell pattern changes from fertilization to time of deposition (see THIÉRY, 1985 for *Triops*; MURA, 1992b for *Chirocephalus diaphanus*). After CO<sub>2</sub> critical point drying, cysts were coated with gold and then observed using a Cambridge Stereoscan 360 at an acceleration voltage of 20 KV and a working distance varying from 9-10 mm for the smaller cysts (clam shrimps) to 25 mm for the bigger ones (*Branchinecta* and tadpole shrimps). Some technical data are given on Fig. 4c.

### MEASUREMENTS

Cyst diameter and surface ornamentation (spines, ridges...) were measured with a SEM numerical point-point system (see example in Figs 4b – crosses, and 4d – vertical lines) and

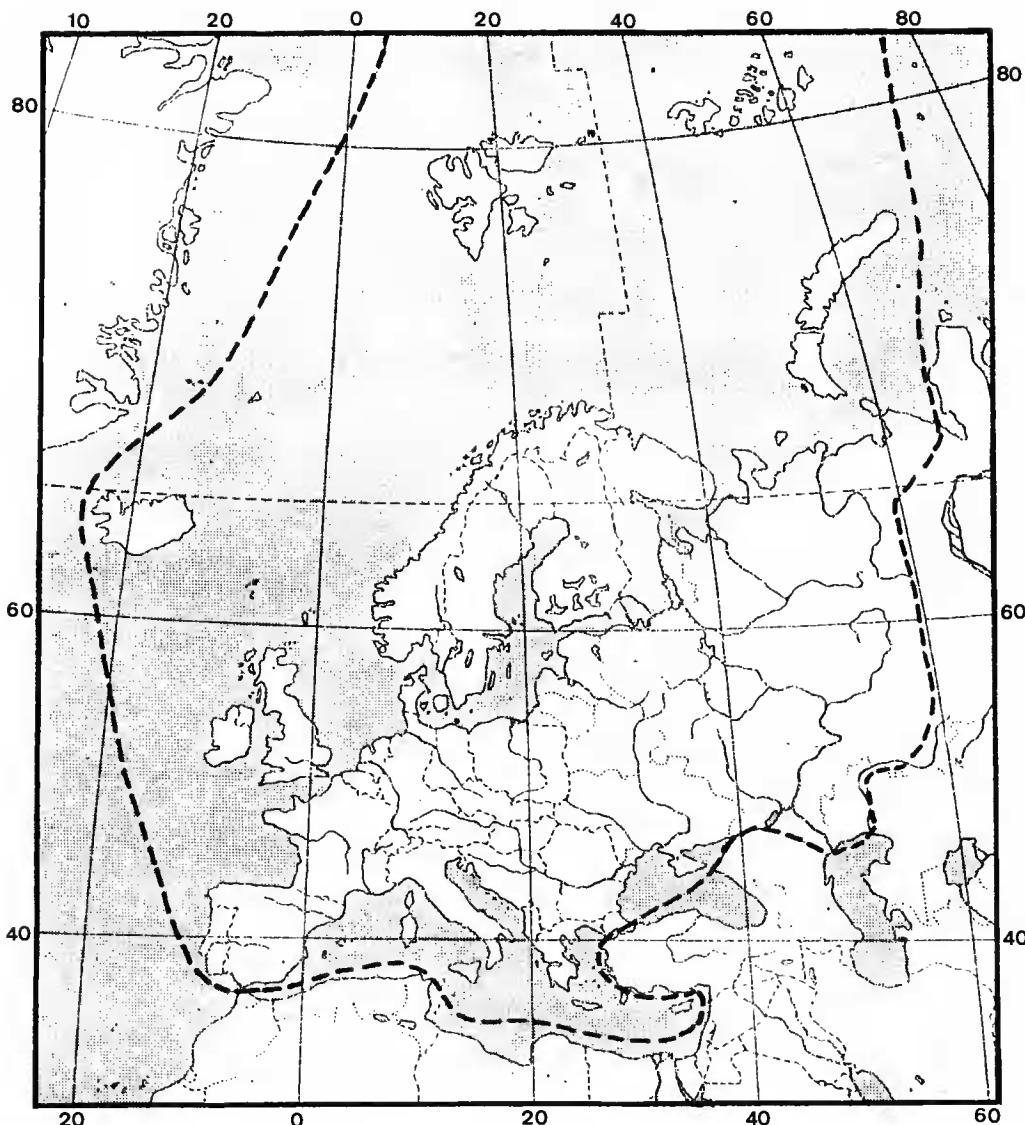


FIG. 1. — Area surveyed in the study of cyst morphology of "large brachiopods".  
*Aire géographique prise en compte pour l'étude de la morphologie des œufs des « grands Branchiopodes ».*

sometimes on calibrated SEM photonegatives. Diameters cited from the literature were measured from published calibrated photographs. To study the variability of cyst diameter we use a Variation Index (V. I.) defined as: maximum diameter-minimum diameter/mean diameter, in per cent.

## MATERIAL EXAMINED

### ANOSTRACA

- Artemia parthenogenetica* Bowen & Sterling, 1978: saltworks of Salin-de-Giraud, Camargue, S. France, 6. 5. 1989, coll. A. THIÉRY (Figs 7h, 8a).
- Artemia tunisiana* Bowen & Sterling, 1978 (= bisexual strain): coastal saltworks, Sète-Villeroy, S. France, 5. 5. 1989, coll. A. THIÉRY (Fig. 8b).
- Branchinecta ferox* (Milne-Edwards, 1840): Hurbanovo, 17. 4. 1956, and Palarikovo, 22. 4. 1969, SW Slovakia, both in coll. J. BRTEK (136) (Figs 4b, c).
- Branchinecta minuta* Smirnov, 1948: Dnepropetrovsk-district, Ukraine, 6. 4. 1937, coll. S. SMIRNOV (Figs 4f, g; 5b-d).
- Branchinecta orientalis* Sars, 1901: Illmitz, Lake Kirchsee, Austria, 26. 5. 1963, coll. J. VORNATSCHER (Fig. 4e).
- Branchinecta paludosa* (Müller, 1788): High Tatra mountains, Horne Furkotske Lake, N. Slovakia. (Figs 4a; 5a).
- Branchinecta tolli* (Sars, 1897): Laptevis Sea, Stolbovoj Island, Russia, 29. 2. 1985, and Tiksi, Yakutia, Russia, 1. 8. 1985, coll. N. VEKHOFF (Figs 4d; 5e-g).
- Branchinectella media* (Schmankevitch, 1873): Troick District, Kudaj-Sugur lake, Kazakhstan, 11. 4. 1932, coll. S. SMIRNOV (Figs 7e; 8e).
- Branchinella spinosa* (Milne-Edwards, 1840): salterns of Salin-de-Giraud, Camargue, Southern France, 6. 5. 1989 (Fig. 8c).
- Branchipus blanchardi* Daday, 1908: High Alps, type locality on the Cristol Plateau, France, 24. 8. 1988, coll. A. THIÉRY (Fig. 6j, k).
- Branchipus schaefferi* Fischer, 1834: Tekovské Luzany (Sec. Kertész 1956 as "Nagysallo", SW Slovakia, 27. 5. 1972, coll. J. BRTEK (1513) syn. *visnyai* (Fig. 6h), and Rivesaltes, 19. 11. 1987, and Plain of Crau, 26. 3. 1994, S. France, coll. A. THIÉRY (Fig. 6i).
- Branchipus laevicornis\** Daday, 1910: Eregli, Asia Minor, coll. E. DADAY, 1912 MNHN Bp273 (Fig. 7d).
- Chirocephalus bairdi\** (Brauer, 1877): Berekhat Hitin, Israel, 24. 3. 1983, coll. R. ORTAL (Fig. 10a-c).
- Chirocephalus chyzeri* (Daday, 1890): Maly Hores, 24. 4. 1970, and Vel'ky Kamenec, SE Slovakia, 24. 4. 1970, coll. J. BRTEK (745, 752) (Fig. 9c, d).
- Chirocephalus carnuntanus* (Brauer, 1877): Gbelce, 28. 4. 1966, and Hurbanovo, 14. 4. 1967, SW Slovakia, coll. J. BRTEK (228) (Figs 9i; 10i-l).
- Chirocephalus diaphanus* Prévost, 1803: Saint-Maximin, S. France (Provence), 7. 2. 1988, coll. A. THIÉRY (Fig. 8j).
- Chirocephalus diaphanus carinatus* (Daday, 1910): Musala, Bulgaria, alt. 2300 m, 8. 8. 1962, coll. J. GULICKA (Fig. 9b).
- Chirocephalus josephinae* (Grube, 1853): Ust'-Kut, Asian Russia, 4. 6. 1925, coll. S. SMIRNOV (Figs 9h; 10h).
- Chirocephalus orghidani* Brtek, 1966: Planitza, Romania, 18. 4. 1960, coll. P. BANARESCU (Figs 8i; 10e).
- Chirocephalus pelagonicus* Petkovski, 1986: Golemo Konjari, Macedonia, 4. 5. 1985, coll. S. PETKOVSKI (Fig. 9a).
- Chirocephalus salinus* (Daday, 1910): "Trepadoules" Porto Vecchio, SE Corsica, 28. 1. 1988, coll. A. THIÉRY (Figs 8k; 10d).
- Chirocephalus shadini* (Smirnov, 1928): Bol'-Zatin, 25. 4. 1970, and Zatin, 15. 4. 1969, SE Slovakia, coll. J. BRTEK (755, 399) (Figs 9g; 10f).
- Chirocephalus slovacicus* Brtek, 1971: Jesenské, 12. 4. 1968, Janice, 22. 4. 1970, and Lenartovce-Vlkyna, 21. 4. 1981, S. Slovakia, coll. J. BRTEK (365, 718, 1873) (Figs 9e; 10g).
- Chirocephalus spinicaudatus* Simon, 1886: France, MNHN Bp157, coll. E. SIMON (25. 96), E. DAOAY det. 1909 (Fig. 9f).
- Drepanosurus birostratus* (Fischer, 1851): Tomsk, Russia, 25. 4. 1919 (Fig. 8h: immature cyst).
- Drepanosurus hankoi* (Dudich, 1927): Kralovsky Chlmec, SE Slovakia, 15. 4. 1969, coll. J. BRTEK (398) (Figs 6a, b; 7a).
- Linderiella massaliensis* Thiéry & Champeau, 1988: Saint-Maximin, S. France, 7. 2. 1988, coll. A. THIÉRY (Figs 7f; 8d).

\* Species living outside the study area, but described for comparison.

*Polyarteuiia forcipata* Fischer, 1851: Murmansk, Russia, 1898 (No 228) (Fig. 7b).

*Siphonophanes grubii* (Dybowski, 1860): Moravia, coll. J. HHRABÉ 27. 4. 1958, MNHN Bp 161, and Slovakia mer-occid. Sv. Jur. 25. 4. 1958 J. BRTEK leg., MNHN Bp 260 (Figs 6f, g; 7c).

*Streptocephalus torvioris* (Waga, 1842): Malé Trakany, 19. 7. 1969, and Dobra, 19. 7. 1969, SE Slovakia, coll. J. BRTEK (545, 552) (Fig. 6c-e).

*Tanymastix stagnalis* (Linnaeus, 1758): Fontainebleau forest, France, 9. 8. 1988, coll. A. THIÉRY (Fig. 8f).

*Tanymastix stellae* Cottarelli, 1968: "Trepadoules" South of Porto Vecchio, Corsica, 28. 1. 1988, coll. A. THIÉRY (Fig. 8g).

#### NOTOSTRACA

*Lepidurus apus* (Linnaeus, 1758): Kamenicnà, SW Slovakia, 14. 5. 1970, coll. J. BRTEK (840); Gavotí, 21. 2. 1988, and Rochefort du Gard, S. France, both in coll. A. THIÉRY (Figs 11e; 12a, d, f-h).

*Lepidurus arcticus* (Pallas, 1793): Sachanika west Coast of Novaya Zemlya, Russia, 12. 9. 1925, coll. Zool. Inst. AN USSR (Fig. 12b, e).

*Lepidurus couesii* Packard, 1875: Ulan Bator, Mongolia, 7. 7. 1970, coll. Z. PEREGI (Fig. 12c).

*Triops cancriformis* (Bosc, 1801): Komárovce, SE Slovakia, 17. 7. 1969, coll. J. BRTEK; Opoul, 26. 3. 1988, and Plain of Crau, 26. 3. 1994, S. France, coll. A. THIÉRY (Fig. 11a-d).

#### SPINICAUDATA

*Limnadia lenticularis* (Linnaeus, 1761): Komarno, 26. 7. 1969, and Kava, 30. 5. 1973, SW Slovakia, coll. J. BRTEK (602) (Fig. 13a-c).

*Imnadia yeyetta* Hertzog, 1935: Sulany, 15. 5. 1970, and Medvedov, 16. 5. 1970, SW Slovakia, coll. J. BRTEK (893) (Fig. 13d, e), and La Galère, Plain of Crau, S. France, 26. 3. 1994, coll. A. THIÉRY.

*Cyclus tetracerus* (Krynicki, 1830): Dobra, 3. 6. 1970, and Jenkovce, 31. 5. 1970, SE Slovakia, coll. J. BRTEK (984, 1065); Gavotí, Provence, S. France, 21. 2. 1988, coll. A. THIÉRY (Fig. 13f, g, i).

*Eocycicus orientalis* Daday, 1913: Astrahan, Russia, 3. 6. 1968. (Fig. 13h, j).

*Leptestheria dahalacensis* (Rüppel, 1837): Sul'any, 15. 5. 1970, and Nové Zámky, 29. 5. 1973, SW Slovakia, coll. J. BRTEK (866, 1779) (Fig. 14a-e).

*Eoleptestheria ticiensis* (Balsamo-Crivelli, 1859): Novosad-Jastrabie, 1. 6. 1970, and Zemplínske Jastrabie-Oborín, 1. 6. 1970, SE Slovakia, coll. J. BRTEK (1005, 1009) (Fig. 14f).

#### LAEVICAUDATA

*Lynceus brachyurus* Müller, 1776: Kralovsky Chlmeč, 3. 6. 1970, SE Slovakia, coll. J. BRTEK (1043) (Fig. 14g, h).

## RESULTS

#### SIZE-DIAMETER

Results are presented in Table I and Fig. 2. In Table I, the species are listed in taxonomic order; in Fig. 2 by increasing size. For each species, our original data (labelled "this study") have been supplemented by data from the literature. In all cases, except where diameters are related to erroneous scale bars, as in Alonso & Alcaraz (1984) for *Branchinecta ferox* and *B. cervantesi* or in Mura (1992, Pl. 2, p. 237) for six species of *Chirocephalus*, the cysts are of more or less consistent diameter. In most cases, our results agree with data in the literature.

In most cases, the Variation Index (VI) ranges from 3 to 30%. However, in several species, such as in *Branchipus schaefferi*, *Tanymastix stagnalis*, *Streptocephalus torvioris*, *Chirocephalus diaphanus*, and *Artemia*, the index is higher, from 30 to 55%. The lesser values of the Variation Index, indicating a relative constancy in cyst diameter whatever the geographical origin of the population, are found in species with restricted areas of distribution, while values of V. I.

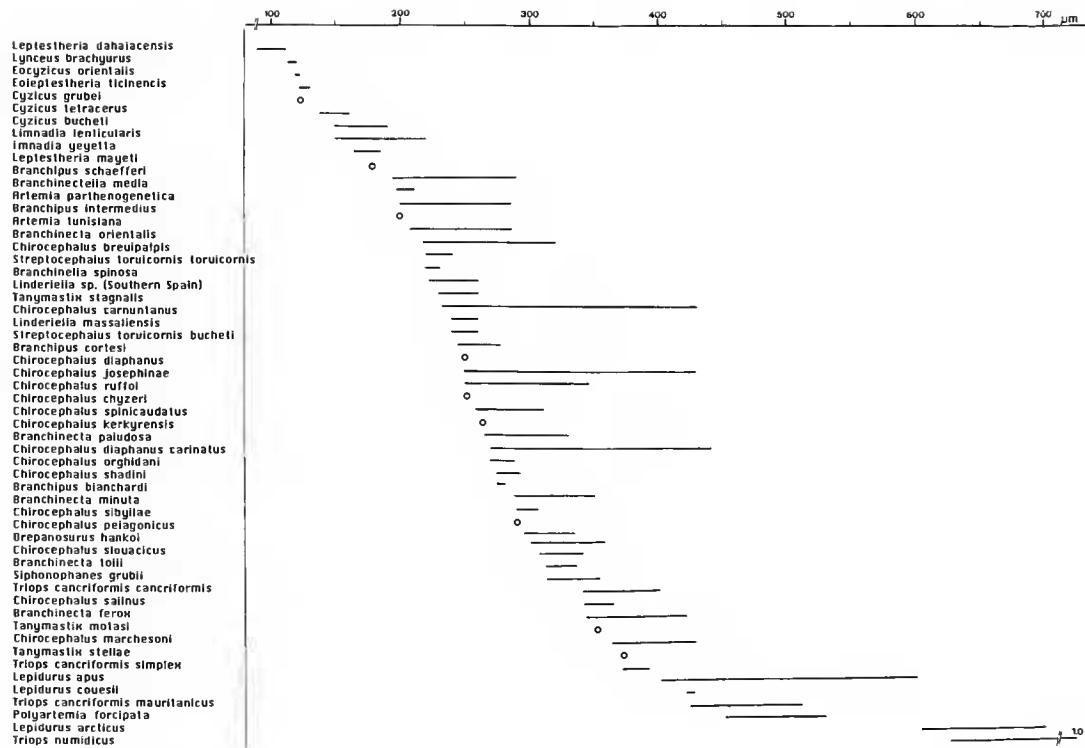


FIG. 2. — Diameters in  $\mu\text{m}$  (low and high values from this paper and from available literature) of the cysts of European brachiopods ranged from the smaller to the larger. Open circles indicate single measurements.

Diamètres en  $\mu\text{m}$  (valeurs inférieures et supérieures d'après les résultats de cette étude et les données bibliographiques) des œufs des Brachiopodes d'Europe classés par ordre croissant de taille. Les cercles indiquent des mesures isolées.

are greater in common and widely distributed species (for geographical distribution in Europe, see BRTEK & THIÉRY, 1995).

The V. I. might be also linked with the diversity of measurements (number of authors or precision of the measurements, as shown in Fig. 3 which illustrates the correlation between the Variation Index and the number of citations in the literature:  $V. I. (\%) = 5.558 \text{ number of citations} + 0.39$  ( $n = 31$ ,  $r^2 = 0.633$ ,  $P < 0.05$ ).

The smallest cysts are those of spinicaudatans and laevicaudatans, ranging from 95 to 209  $\mu\text{m}$ . Those of anostracans range from 198 to 527  $\mu\text{m}$  and of notostracans from 350 to 780  $\mu\text{m}$ . The Arctic species *Polyartemia forcipata* and *Lepidurus arcticus* have the largest cysts of the European "large brachiopods".

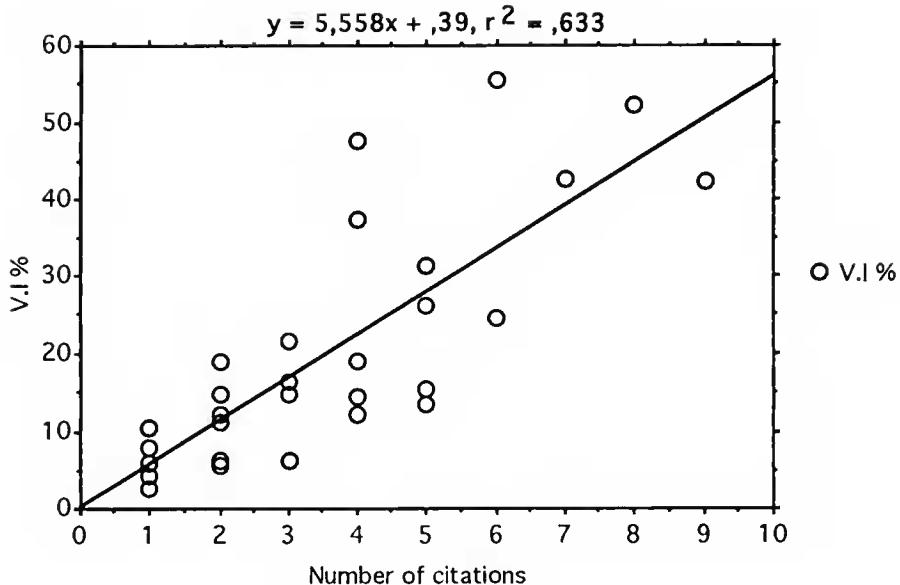


FIG. 3. — Relation between variation index (%) and number of citations in the literature. V. I. % = 5.558 citations + 0.39 ( $n = 31, r^2 = 0.633, P < 0.05$ ).

Relation entre l'indice de variation (en %) et le nombre de références dans la littérature. V. I. (%) = 5,558 citations + 0,39 ( $n = 31, r^2 = 0,633, P < 0,05$ ).

#### CYST MORPHOLOGY

ANOSTRACA (Table I and Figs 4 to 14): except for the cysts of the genus *Tanymastix* which are lenticular, all those of anostracans are more or less spherical. Their surface may be smooth, as in *Artemia* and *Branchinectella media*, or, more usually ornamented by ridges, spines, depressions or crests.

Polyartemiidae (Fig. 7b): *Polyartemia forcipata* has a large spherical cyst, with a rugose surface, with rounded spines shorter than 10 µm in length, as described by MURA (1992b, Plate 5.3).

Branchinectidae (Figs 4, 5): except for those of *Branchinecta tolli* which are slightly rugose (Figs 4d; 5e, f, g), the cysts of the European species of *Branchinecta* are characterized by low ridges which delineate large polygons (Figs 4a-c, e-g; 5a, b). (GILCHRIST, 1978; MURA & THIÉRY, 1986; MURA, 1991a, and MAEDA-MARTINEZ *et al.*, 1992, 1993). The cysts of *Branchinecta paludosa* and *B. ferox* are similar in appearance and of the same size, but the polygonal areas tend to be larger in the former. Likewise the cysts of *Branchinecta orientalis* and *B. minuta* are very similar (Fig. 4e, f, g). They are smaller than those of *B. paludosa* and *B. ferox*, and their ridges are more rounded and delineate smaller polygonal areas. No objective character distinguishes them. Concerning the internal structure of the egg-shell, its spongy aspect in *Branchinecta*

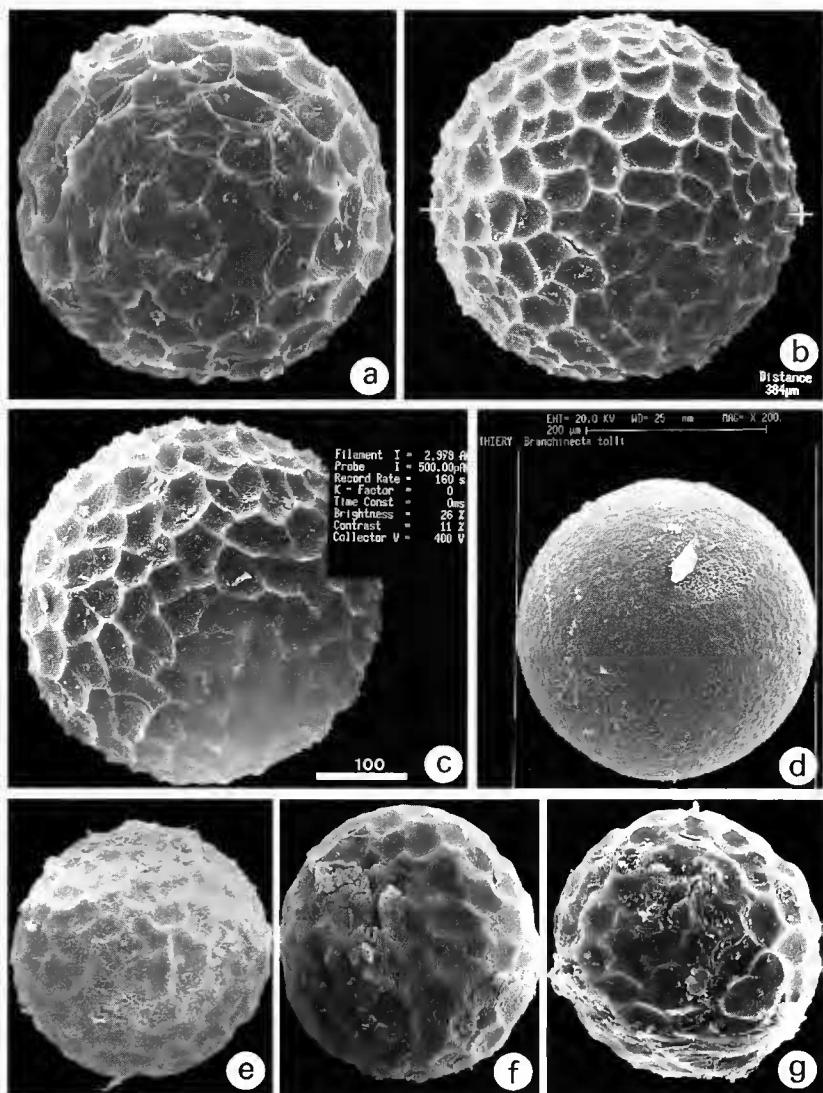


FIG. 4. — Cysts of anostraca: a) *Branchinecta paludosa*; b), c) *B. ferox*; d) *B. tolli*; e) *B. orientalis*; f), g) *B. minuta*. (common scale bar in  $\mu\text{m}$ ).

(Œufs d'Anostraca: a) *Branchinecta paludosa*; b), c) *B. ferox*; d) *B. tolli*; e) *B. orientalis*; f), g) *B. minuta* (échelle commune en  $\mu\text{m}$ ).

*minuta* (Fig. 5c, d), agrees with the findings of GILCHRIST (1978) for *B. ferox*. In *B. tolli*, the cyst wall is thin with thick low roots (Fig. 5f). No data are available for *B. orientalis*.

Artemiidae (Figs 7, 8): cysts of *Artemia* are spherical and smooth (Figs 7h; 8a, b), as described in many studies (MAZZINI, 1978; GILCHRIST, 1978; MURA & THIÉRY, 1986; SPOTTE &

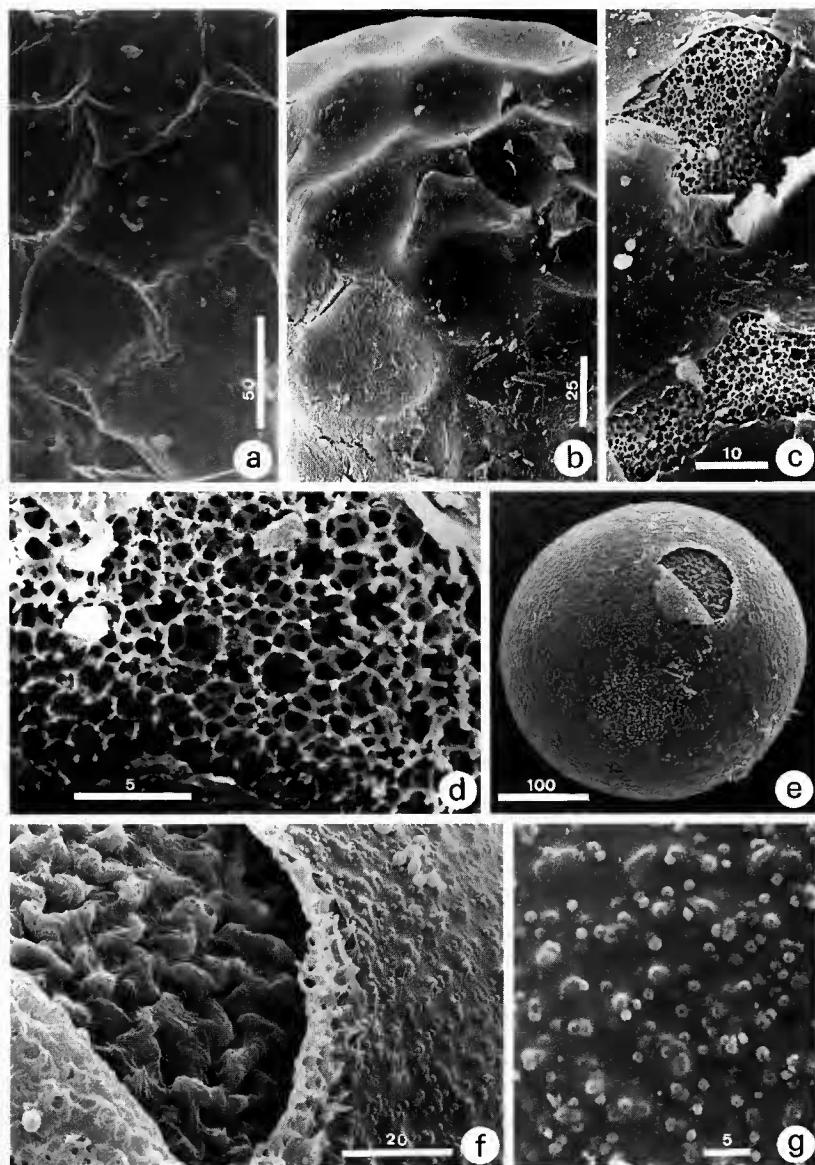


FIG. 5. — Cysts of Anostraca: a) details of *Branchinecta paludosa*, b) idem, *B. minuta*, c) idem, outer membrane cracked showing spongy structure; d) detail of spongy structure; e) *Branchinecta tolli*, f) *Branchinecta tolli*, detail of a cracked part of egg shell; g) *B. tolli*, detail of surface showing little rounded pits. (scale bars in  $\mu\text{m}$ ).

*Oeufs d'Anostraca : a) détail, Branchinecta paludosa ; b) idem, B. minuta ; c) B. minuta, la membrane externe déchirée permet de voir la structure spongieuse ; d) B. minuta, détail de la structure spongieuse ; e) Branchinecta tolli ; f) B. tolli, détail de la partie déchirée de l'enveloppe ; g) B. tolli, détail de la surface montrant les petits tubercules (échelles en  $\mu\text{m}$ ).*

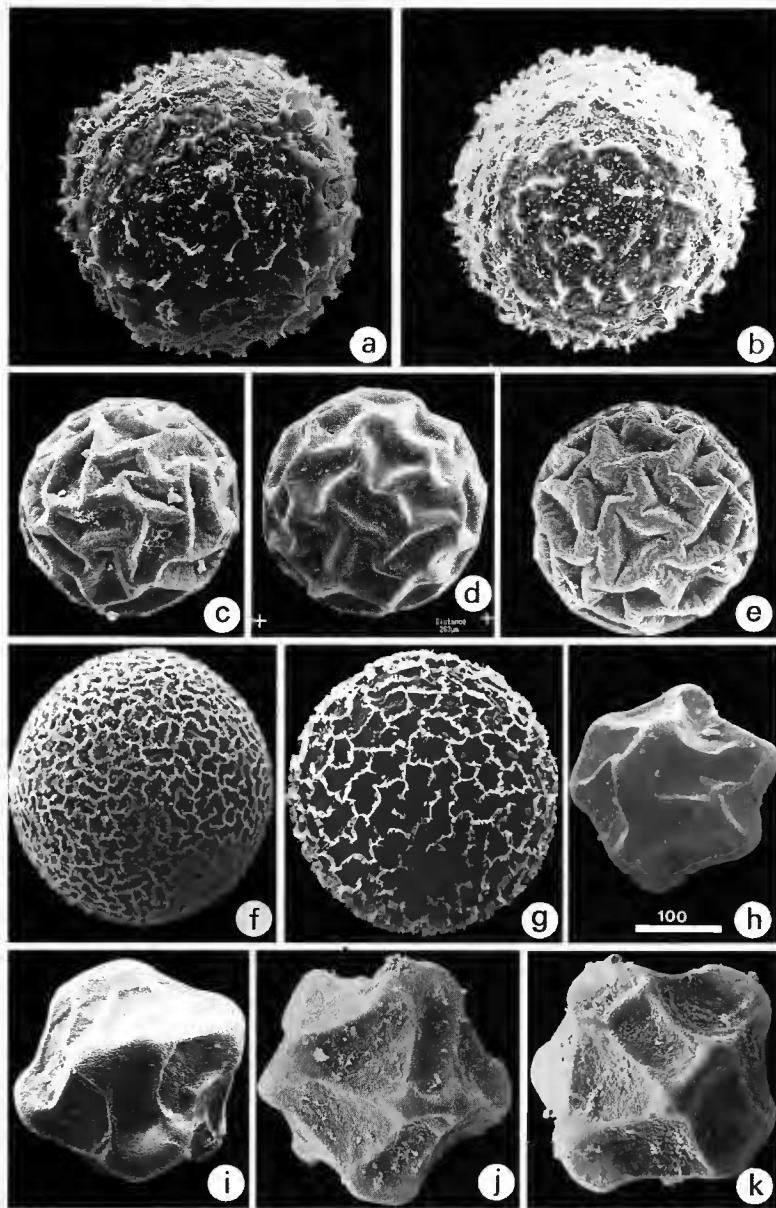


FIG. 6. — Cysts of Anostraca: a), b) *Drepanosurus hankoi*; c), d), e) *Streptocephalus torvicornis*; f), g) *Siphonophanes grubii*; h) *Branchipus schaefferi* syn. *visnyai*; i) *Branchipus schaefferi*; j), k) *Branchipus blanchardi* (common scale bar in  $\mu\text{m}$ ).

Oufs d'Anostraca : a) et b) *Drepanosurus hankoi* ; c), d), e) *Streptocephalus torvicornis* ; f), g) *Siphonophanes grubii* ; h) *Branchipus schaefferi* syn. *visnyai* ; i) *Branchipus schaefferi* ; j), k) *Branchipus blanchardi* (échelle commune en  $\mu\text{m}$ ).

ANDERSON, 1988; THIÉRY & GASC, 1991). Except for a small difference in size, no objective distinction exists between the cysts of the parthenogenetic and bisexual strains. The vitelline envelope is thin and spongy (Fig. 7h).

Branchipodidae (Figs 6, 7, 8): this family presents two very different patterns: lenticular cysts in *Tanymastix* (Figs 7g; 8f, g) (only small and often unreliable differences between the species) and wrinkled and angulated in *Branchipus* (Fig. 6h-k). The cysts of *Branchipus schäfferi* and *B. blanchardi* are shown in this paper while that of *B. cortesi* is illustrated in ALONSO & JAUME (1991, Fig. 4b, c, p. 227). As in *Tanymastix*, whose cyst pattern can be considered as generic, the angulated shape of *Branchipus* cysts is so similar in the four European species that we suggest that it could be generic also. This is confirmed by the cyst of *Branchipus laevicornis*, the fifth species of the genus, living in Asia minor, which is very similar in shape to that of the three species studied (Fig. 7d) and that studied by ALONSO & JAUME (1991). The differences between these species are hardly distinguishable without a large series permitting study of the morphology and size variability. This pattern is found also in a thamnocephalid, *Dendrocephalus spartaenovae* (MURA, 1992b, Plate 6.3), but this is a South American species, so no confusion is possible in field studies. In section the alveolar layer of the cyst wall of *Branchipus blanchardi* and *B. laevicornis* (both unpublished), are spongy as in *B. schäfferi* (KUPKA, 1940, Figs 6-11; GILCHRIST, 1978, Figs 1c, d, 2a-d). In addition, the outer surface has numerous pores in *B. blanchardi* (THIÉRY & GASC, 1991, Fig. 32), *B. laevicornis* (unpublished) and *B. schäfferi* (KUPKA, 1940, Fig. 5; GILCHRIST, 1978, Fig. 1b; MURA & THIÉRY, 1986, Pl. IV.B).

Thamnocephalidae (Fig. 8): the cyst of *Branchinella spinosa* is spherical with a surface showing an irregular polygonal pattern formed by low mound-like ridges. These ridges are more or less pronounced (in relation to the maturation of the egg shell). Cyst size is close to that of *Artemia* (which always has smooth cysts), with which this species could coexist in coastal saline waters as in the Camargue and Sardinia. The *B. spinosa* pattern is constant for all populations observed (ALONSO & ALCARAZ, 1984, Fig. 2.d; MURA, 1986, Plate 5.a; 1992b, Plate 1.5; MURA & THIÉRY, 1986, Plate II.a).

Streptocephalidae (Fig. 6): cysts of *Streptocephalus torvicornis* are well known (VALOUSEK, 1952; ALONSO & ALCARAZ, 1984; MURA & THIÉRY, 1986; THIÉRY, 1987; THIÉRY & GASC, 1991; DE WALSCHÉ *et al.*, 1991; MURA, 1992b). They have a “folded look” with polygonal cells irregularly shaped by raised ridges (Fig. 6c-e). Cysts of *Streptocephalus torvicornis bucheti* are similar to those of *S. t. torvicornis* (ALONSO & ALCARAZ, 1984, and MURA & THIÉRY, 1986).

Linderiellidae (Figs 7, 8): the cysts of the genus *Linderiella* are spiny (Fig. 8d), even with acute spines (15-20 µm long) in the French *Linderiella massaliensis* (Fig. 7f), or with flat trumpet tips in the Spanish form (ALONSO & ALCARAZ, 1984; THIÉRY & CHAMPEAU, 1988). In all cases the spines are different from those of the spiny cysts of some species of *Chirocephalus*, where they arise from the crests of honeycomb-like surface of the shell. In *Linderiella* they arise directly from the shell.

Chirocephalidae Chirocephalinae (Figs 8, 9, 10): at first glance cysts of *Chirocephalus* species present great heterogeneity. Some are smooth, e.g. *Chirocephalus marchesonii* (MURA *et al.*, 1978, Pl. 1; MURA, 1986, Pl. 4), some spiny, e.g. *C. ruffoi* (MURA, 1986, Pl. 12), *C. diaphanus carinatus* (Fig. 9b) and *C. carnuntatus* (Fig. 9i), some more or less bumpy as *C. chyzeri* (Fig. 9c, d),

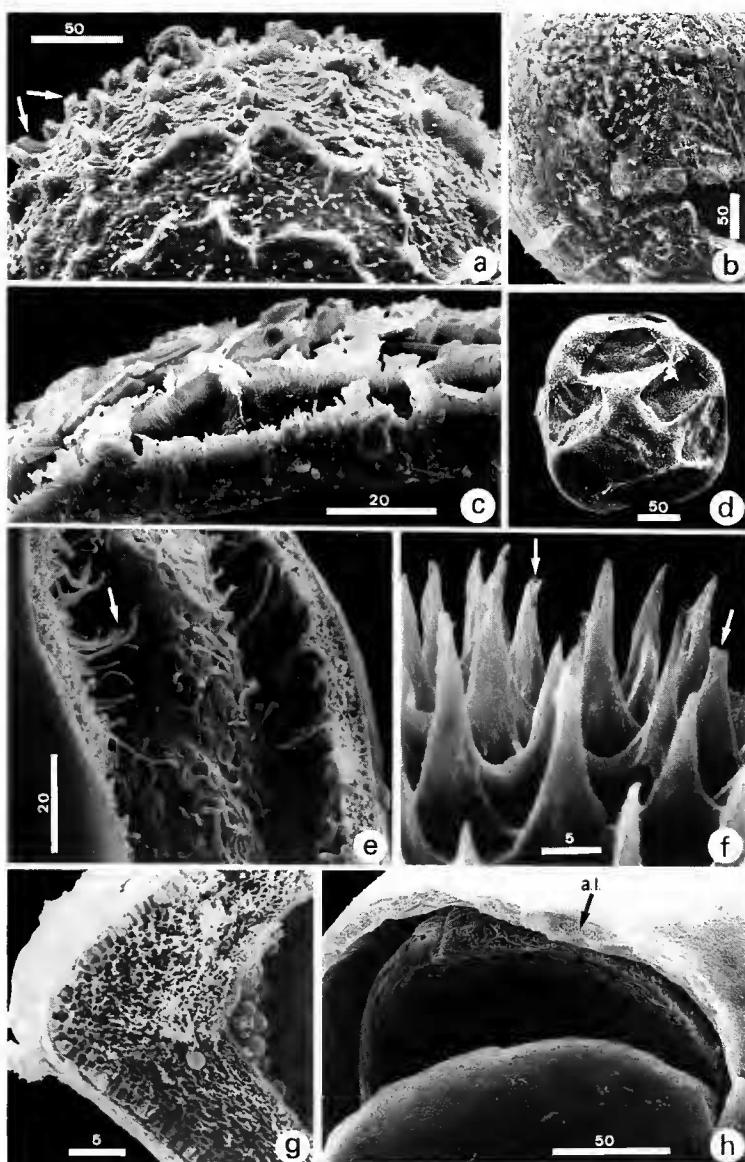


FIG. 7. — Details of the cysts of Anostraca: a) *Drepanosurus hankoi* — see low ridges (arrows); b) *Polyartemia forcipata* — see small spines (arrows); c) *Siphonophanes grubii*; d) whole cyst, *Branchipus laevicornis*; e) internal view of envelope, *Branchinectella media* (see the pillars — arrow); f) spines of *Linderiella massaliensis* (those marked with an arrow are broken); g) section, *Tanymastix stagnalis*, showing spongy structure; h) detail of the envelope, *Artemia* (a.l. — alveolar layer). (Scale bars in  $\mu\text{m}$ .)

Détails des œufs d'Anostraca : a) *Drepanosurus hankoi* — voir les ridges (flèches) ; b) *Polyartemia forcipata* — noter les petites épines (flèches) ; c) *Siphonophanes grubii* ; d) œuf de *Branchipus laevicornis* ; e) vue interne de l'enveloppe chez *Branchinectella media* (noter les filaments — flèche) ; f) épines de *Linderiella massaliensis* (celles marquées d'une flèche sont cassées) ; g) coupe transversale de l'œuf de *Tanymastix stagnalis* montrant la structure spongieuse ; h) détail de l'enveloppe d'*Artemia* (a. l. — couche alvéolaire). (Échelles en  $\mu\text{m}$ .)

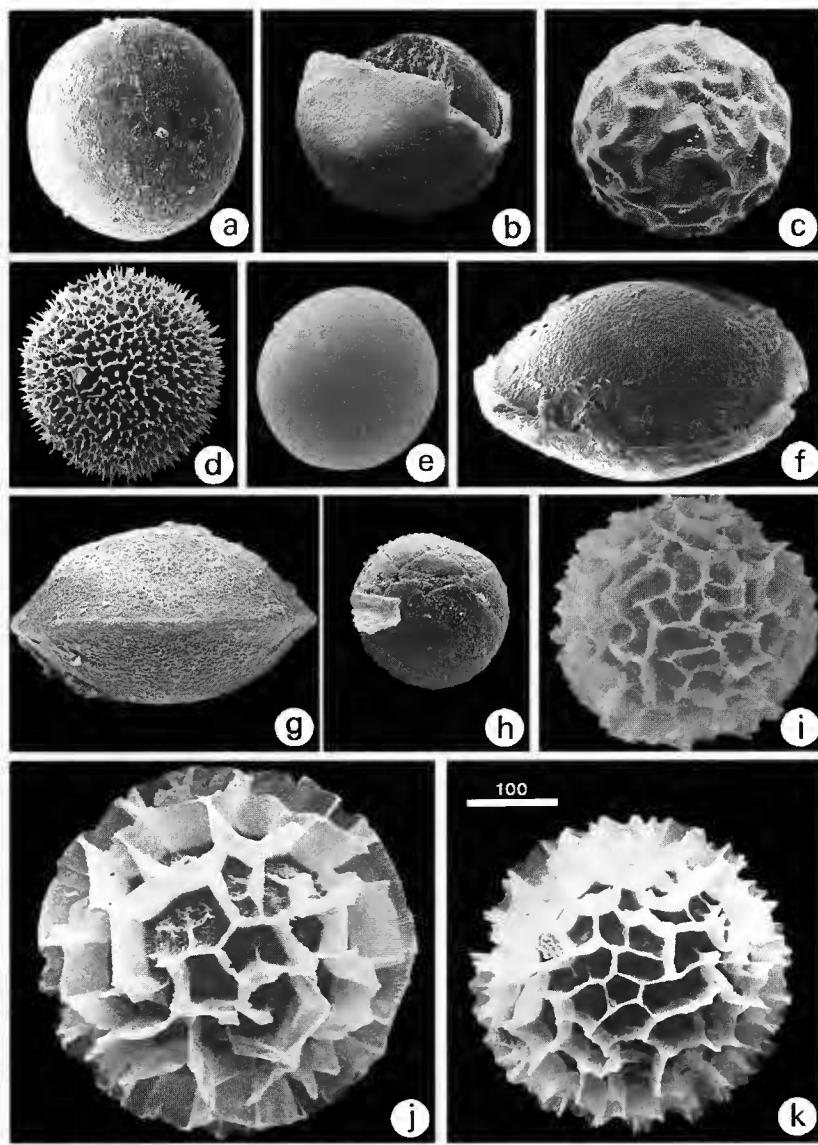


FIG. 8. — Cysts of Anostraca: a) *Artemia* (bisexual strain); b) *idem*, cracked cyst; c) *Branchinella spinosa*; d) *Linderiella massaliensis*; e) *Branchinectella media*; f) *Tanymastix stellae*; g) *Tanymastix stagnalis*; h) immature cyst, *Drepanosurus birostratus*; i) *Chirocephalus orghidani*; j) *Chirocephalus diaphanus*; k) *Chirocephalus salinus* (common scale bar in  $\mu\text{m}$ ).

*Oeufs d'Anostraca : Artemia (souche bisexuée) ; b) idem, œuf déchiré ; c) Branchinella spinosa ; d) Linderiella massaliensis ; e) Branchinectella media ; f) Tanymastix stellae ; g) Tanymastix stagnalis ; h) œuf immature, Drepanosurus birostratus ; i) Chirocephalus orghidani ; j) Chirocephalus diaphanus ; k) Chirocephalus salinus (échelle commune en  $\mu\text{m}$ ).*

*C. slovacicus* (Fig. 9e), *C. spinicaudatus* (Fig. 9f), *C. shadini* (Fig. 9g), and *C. josephinae* (Fig. 9h), or have thin and high ridges in *C. orghidani* (Fig. 8i), *C. diaphanus* (Fig. 8j), *C. salinus* (Fig. 8k), and *C. pelagonicus* (Fig. 9a). As far as grouping distinctions are concerned (see BRTEK & THIÉRY, 1995), a typical pattern seems to be dominant in each *Chirocephalus* group. In the *bairdi*-group (4 species), three species (*C. orghidani* – this paper, Fig. 8i; *C. brevipalpis* – PETKOVSKI 1991a, Fig. 1e; and *C. kerkyrensis* – MURA *et al.*, 1978, Pl. 4; MURA, 1986, Pl. 10; 1992b, Pl. 2.1, 2) have a pattern of polygonal areas formed by high and thin crests. This pattern is also present in *Chirocephalus bairdi* (Fig. 10a-c), a species of the Levant. Cysts of the last

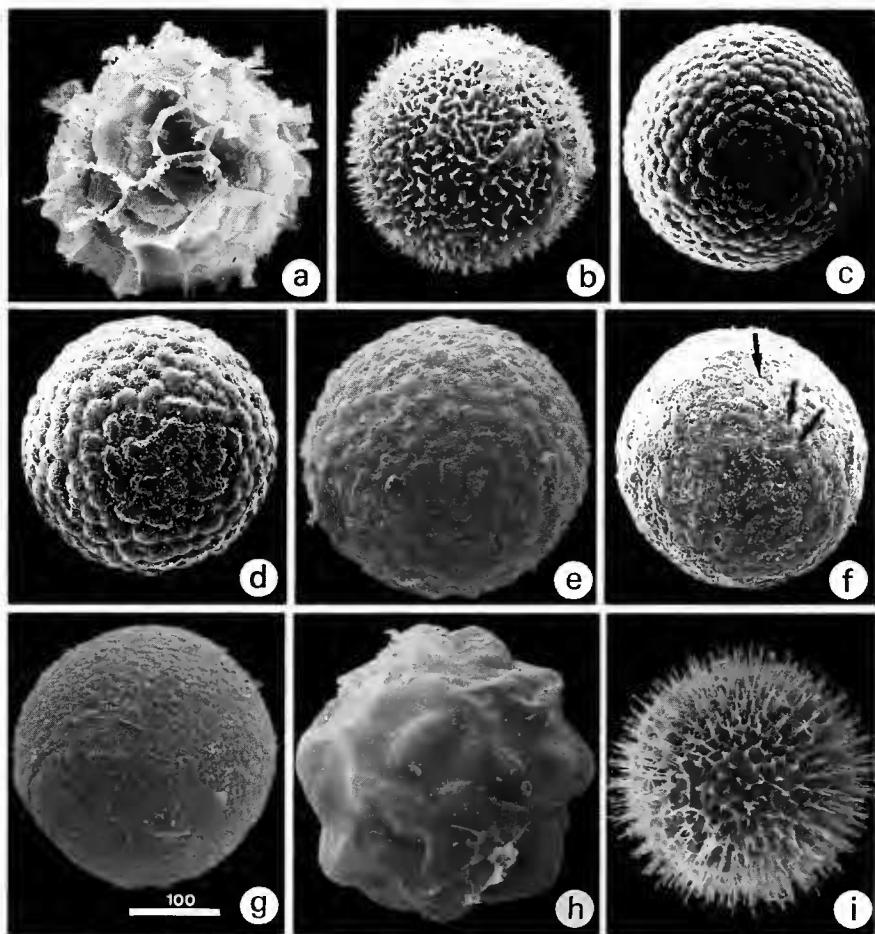


FIG. 9. — Cysts of Anostraca: a) *Chirocephalus pelagonicus*; b) *Chirocephalus diaphanus carinatus*; c), d) *C. chyzeri*; e) *C. slovacicus*; f) *C. spinicaudatus* (note the verucose aspect under the external crust, arrows); g) *C. shadini*; h) *C. josephinae*; i) *C. carnuntanus* (common scale bar in  $\mu\text{m}$ ).

(Œufs d'Anostraca : a) *Chirocephalus pelagonicus*; b) *Chirocephalus diaphanus carinatus*; c), d) *C. chyzeri*; e) *C. slovacicus*; f) *C. spinicaudatus* (noter l'aspect verruqueux, flèches); g) *C. shadini*; h) *C. josephinae*; i) *C. carnuntanus* (échelle commune en  $\mu\text{m}$ ).

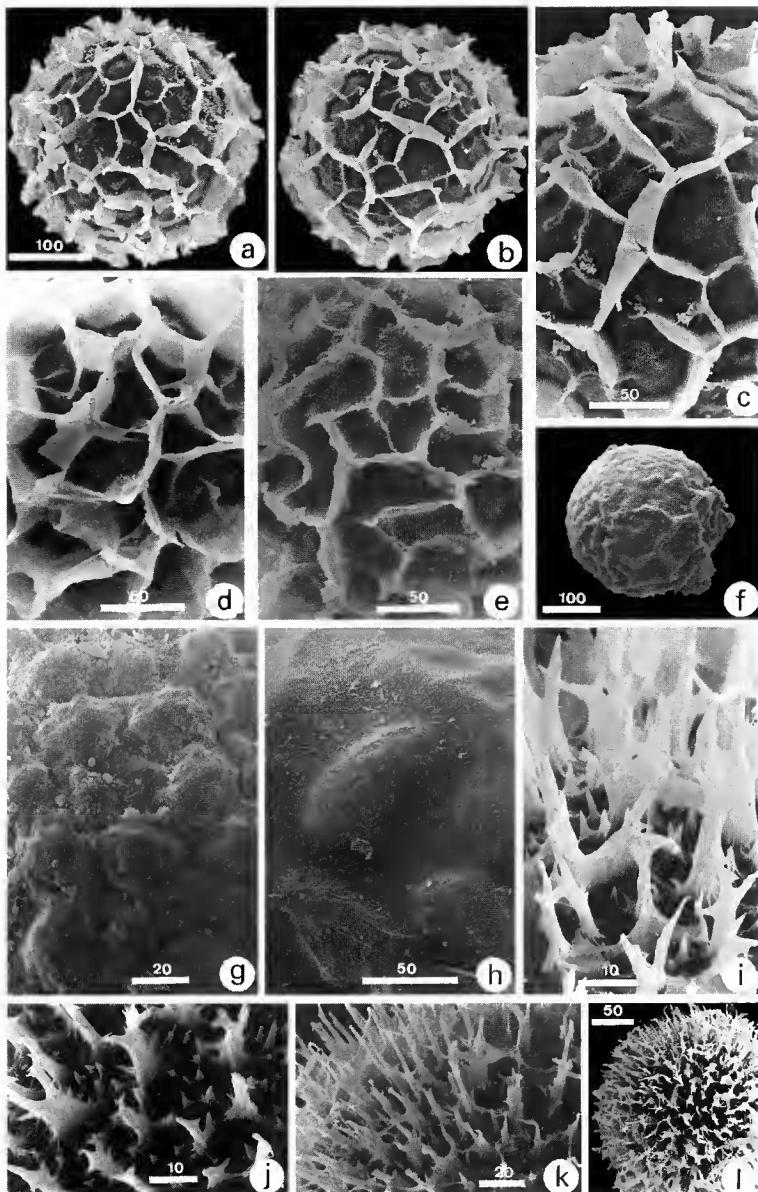


FIG. 10. — Cysts of Anostraca: a), b) *Chirocephalus bairdi*; c) *C. bairdi*, detail of the surface; d) *C. salinus*, detail; e) *C. orghidani*, detail; f) *C. shadini*, (cf. Fig. 9g for minor differences); g) *C. slovacicus*; h) *C. josephinae*; i), j), k), l) spines of *Chirocephalus carnuntanus* (scale bars in  $\mu\text{m}$ ).

Oeufs d'Anostraca: a), b) *Chirocephalus bairdi*; c) *C. bairdi*, détail de la surface; d) *C. salinus*, détail; e) *C. orghidani*, détail; f) *C. shadini* (voir fig. 9g pour des petites différences); g) *C. slovacicus*; h) *C. josephinae*; i), j), k), l) épines de l'œuf de *Chirocephalus carnuntanus* (échelles en  $\mu\text{m}$ ).

species, *C. vornatscheri*, are unknown. In the *diaphanus*-group (8 species), a cyst surface pattern of the type already described for the *bairdi*-group, is found in four species (*C. diaphanus*, *C. salinus*, *C. pelagonicus* – this paper, Figs 8j, k; 9a, and *C. sibyllae* – MURA, 1986, Pl. 9.b, and 1992b, Pl. 2.7). A spiny appearance is observed in two species (*C. diaphanus carinatus* – this paper, and *C. ruffoi* – MURA, 1986, Pls 12 and 13.a, and 1992b, Pl. 2.8, Pl. 5.6), while only one has a smooth aspect (*C. marchesonii* – MURA, 1986, Pl. 4, 1992b, Pl. 2.9). Cysts of *C. reiseri* are unknown. The *pristicephalus*-group (4 species) is more heterogeneous with one spiny cyst (*C. carnuntanus*, Figs 9i; 10i, j, k, l), one slightly verrucose (*C. shadini*, Fig. 9g), or sometimes more verrucose (Fig. 10f), and a cyst clearly bumpy (*C. josephinae*, Figs 9h, 10h). The spines of *Chirocephalus carnuntanus* differ from those of *C. diaphanus carinatus*, *Linderiella massaliensis*, and *C. ruffoi* (see MURA, 1986, Pls 12.b, 13.a) by their length and their “trident” aspect in their distal border (Fig. 10i-k). Cysts of the fourth species, *Chirocephalus ripophilus*, remain unknown. In the *spinicaudatus*-group (6 species), three cysts have a verrucose aspect (*C. spinicaudatus*, Fig. 9f; *C. chyzeri*, Fig. 9c, d; and *C. slovacicus*, Figs 9e; 10g); those of *C. croaticus*, *horribilis*, and *robustus*, are unknown.

Chirocephalidae Eubranchipodinae (Figs 6, 7, 8): cysts of *Drepanosurus hankoi* are spherical with irregular, unconnected low ridges or vertical lamellae, 10-15 µm high, non converging and situated without any regularity (Fig. 7a). The surface is also rugose. This pattern is described by MURA (1992b, Plate 5.2). As we could study the cyst of only one of the three European species of *Drepanosurus*, nothing can be said about the generic pattern, but we can note that the pattern found in *D. hankoi* agrees with DADAY's description (1910, Fig. 33g, 1, p. 244) of *D. birostratus* whose cysts are *ova superficie spinulosa, spinulis bacilliformibus*. The cysts of *D. birostratus* described in the present study (Fig. 8h) are immature. No data are available for *D. vladimiri*.

Cyst of *Siphonophanes grubii* somewhat resemble those of *Drepanosurus hankoi* but with thin wrinkled low ribs, connected to one another (Fig. 6f, g), and arranged in a dense complex coral-like network delineating small irregular areas. The wrinkled ribs are 14-17 µm high (Fig. 7c). (see earlier descriptions made by THIÉRY & GASC, 1991, Fig. 14, and MURA, 1992b, Plate 5.1).

Chirocephalidae Branchinectellinae (Figs 7, 8): cysts of *Branchinectella media* are smooth (Figs 7e; 8e; ALONSO & ALCARAZ, 1984, Fig. 2.e) and superficially similar to those of *Artemia*. The structure of the shell, however, is clearly different, with an inner alveolar layer which consists of vertical strands approximately 15 µm long and 1-2 µm thick (Fig. 7e), while in *Artemia* it is only spongy (Fig. 7h).

NOTOSTRACA. Triopsidae (Figs 11, 12): cysts are spherical with a smooth or finely rugose surface. Only the diameter can be used in identification but variation within each species (V. I. from 13 to 26%), makes distinction difficult, particularly between *Triops cancriformis* and *Lepidurus couesii* or between *Lepidurus couesii* and *L. apus*.

Notostracans have the largest resting eggs with spherical cyst up to 400 µm in diameter (Fig. 12). *Triops cancriformis*, *Lepidurus couesii* and *L. apus* have the smallest cysts with respectively diameters of 350-400 µm, 425 µm and 430-520 µm. *Lepidurus arcticus* cysts are larger (603-621 µm) and have a rough surface while those of *Lepidurus apus*, *L. couesii* and *Triops cancriformis* are smooth (Figs 11, 12). The alveolar envelope is also thinner than in other

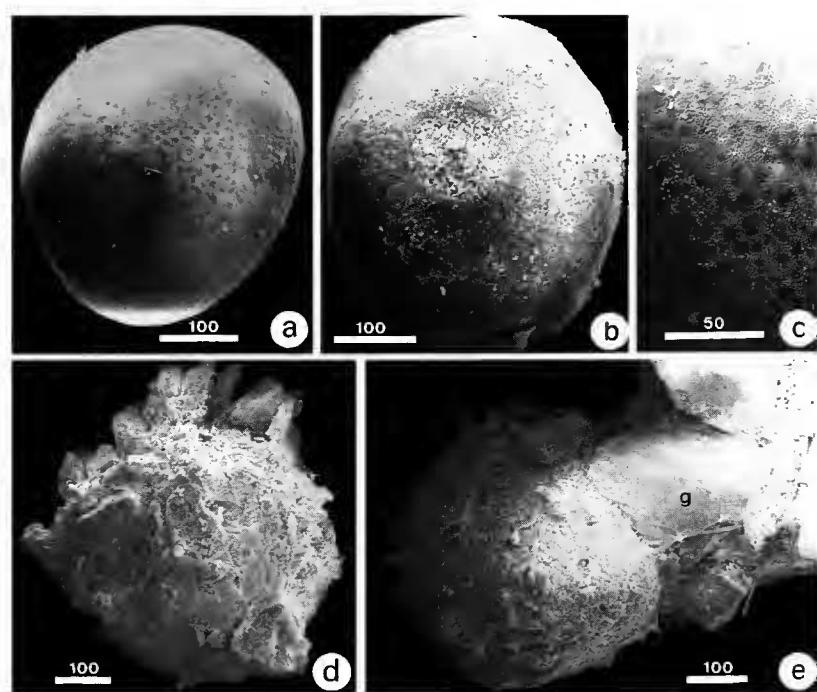


FIG. 11. — Cysts of Notostraca: a), b) *Triops cancriformis*; c) idem, detail of surface; d) idem, cysts stuck on gravel; e) *Lepidurus apus*, cyst stuck on gravel (g). (Scale bars in  $\mu\text{m}$ .)  
Œufs de Notostraca : a), b) *Triops cancriformis*; c) idem, détail de la surface; d) idem, œuf collé à des graviers; e) *Lepidurus apus*, œuf collé sur un gravier (g). (Échelles en  $\mu\text{m}$ .)

notostracans (from 25 to 70  $\mu\text{m}$ ) while the alveolar layer reaches sometimes 110  $\mu\text{m}$ . As reported by THIÉRY (1985) and FRYER (1988) cysts are mostly covered with sediments and gravels (Fig. 11d, e).

Cysts of the Afro-Asian *Triops numidicus*, penetrating Europe only in Sicily and Majorca, is not illustrated here. A description is given in THIÉRY (1985, 1995), and THIÉRY (in press) (spherical and smooth cyst, diameter 610-740  $\mu\text{m}$ ).

SPINICAUDATA (Figs 13, 14). Cyzicidae (Fig. 13): cysts of *Cyzicus* species are spherical, smooth with a very thin membrane ( $< 2 \mu\text{m}$ ) covering a network of thin radiating and entangled setules (Fig. 13f, g, i) approximately 0.4  $\mu\text{m}$  thick and 10-15  $\mu\text{m}$  long (= the vitelline envelope sensu TOMMASINI & SCANABISI SABELLI, 1989). The membrane is sometimes cracked (Fig. 13f, i) allowing the setose envelope to be observed without any treatment. As discussed by THIÉRY & GASC (1991) and THIÉRY (1995), this egg shell structure can be considered generic. For other descriptions of *Cyzicus* cysts see DADAY (1914: *Cyzicus tetracerus*); ALONSO & ALCARAZ (1984: *Cyzicus grubei*), THIÉRY (in press: *Cyzicus gihoni*), and THIÉRY (in prep.: *Cyzicus bucheti*).

*Eocyzicus* has a different egg shell pattern. The external surface of *E. orientalis* cyst is bumpy (Fig. 13h, j), as described by DADAY (1914: *Ova membrana concinna granulata tecta*).

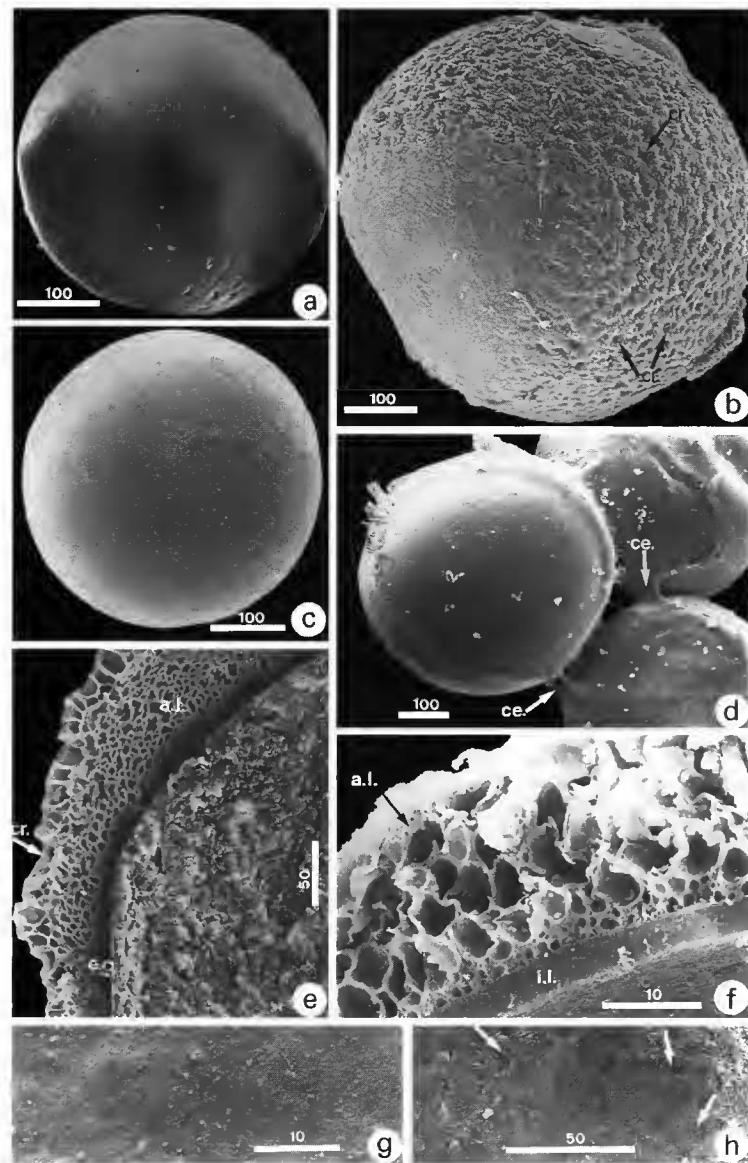


FIG. 12. — Cysts of Notostraca: a) *Lepidurus apus*; b) surface of the cyst of *Lepidurus arcticus* with numerous craters (cr.); c) *Lepidurus couesi*; d) cysts of *Lepidurus apus* glued together by cement (ce.); e) *L. arcticus*, cross section of wall showing alveolar layer (a.l.), embryonic cuticle (e.c.), crater (cr.); f) *L. apus*, section of cyst wall with alveolar layer (a.l.), inner layer (i.l.); g, h) surface of *L. apus* cysts showing in h) the obliterated craters (arrows). (Scale bars in  $\mu\text{m}$ .)

*Oufs de Notostraca : a) Lepidurus apus, b) Lepidurus arcticus, noter la présence de cratères (c.r.) en surface ; c) Lepidurus couesi ; d) œufs de Lepidurus apus agglutinés par un cément (ce.) ; e) L. arcticus, coupe transversale de la paroi montrant la couche alvéolaire (a.l.), la cuticule embryonnaire (e.c.) et les cratères (cr.) ; f) L. apus, coupe transversale de la paroi, couche alvéolaire (a.l.), couche interne (i.l.) ; g, h) surface des œufs de L. apus montrant (en h)) des cratères oblitérés (flèches). (Échelles en  $\mu\text{m}$ ).*

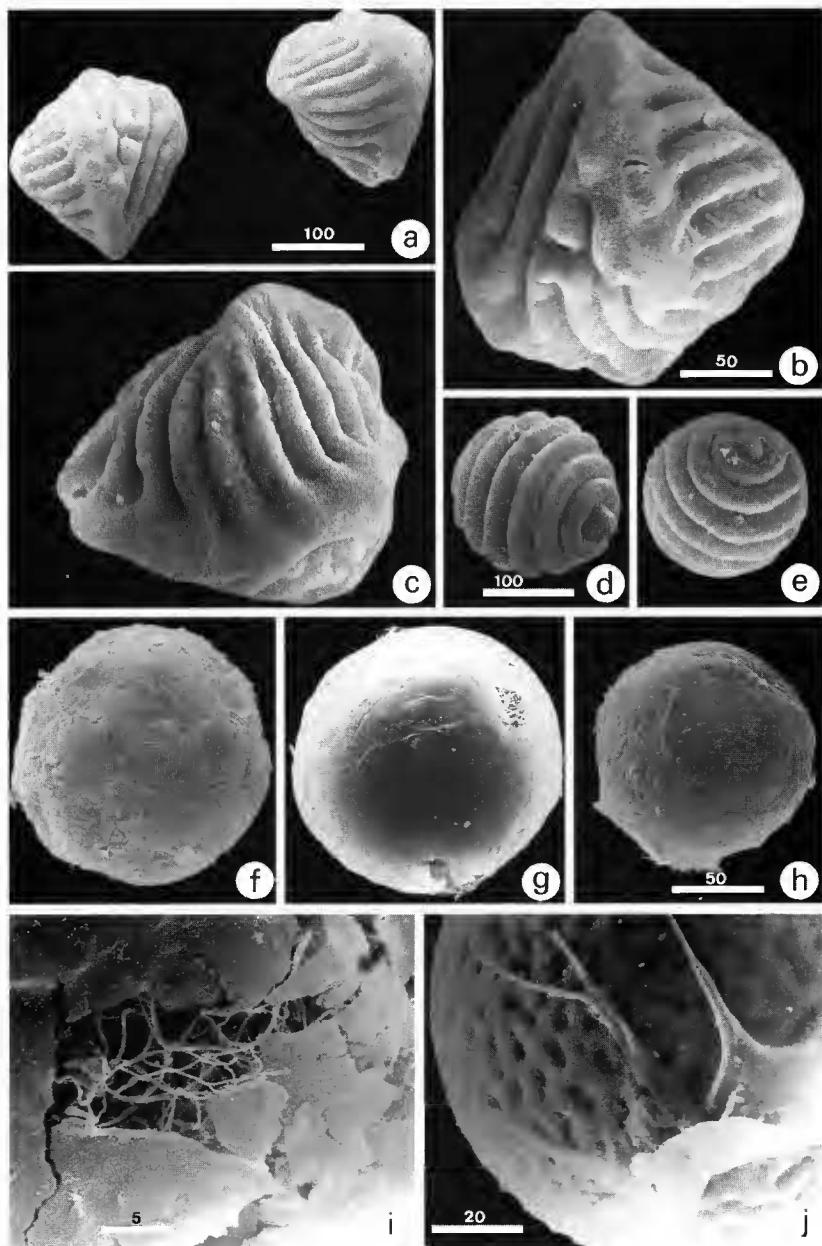


FIG. 13. — Cysts of conchostracans (Spinicaudata): a), b), c) *Limnadia lenticularis* (b), c): same scale); d), e) *Immadnia yeyetta* (same scale); f), g) *Cyzicus tetracerus*; h) *Eocyzicus orientalis* (f), g), h): same scale); i) cracked egg shell, *C. tetracerus*; j) outer surface, *E. orientalis*. (scale bars in  $\mu\text{m}$ ).

(Œufs de conchostracés (Spinicaudata): a), b), c) *Limnadia lenticularis* (b), c): même échelle); d), e) *Immadnia yeyetta* (même échelle); f), g) *Cyzicus tetracerus*; h) *Eocyzicus orientalis* (f), g), h): même échelle); i) enveloppe externe déchirée de *C. tetracerus*; j) surface externe de *E. orientalis* (échelles en  $\mu\text{m}$ ).

A similar pattern has been described for other species of the genus by SAMYIAH *et al.* (1985; = *Caenestheriella*), and THIÉRY (1987; 1995). Cysts of *Eocyzicus propinquus*, *E. skorikowi* and *E. tadei* were not available for our study.

Leptestheriidae (Fig. 14): cysts of *Leptestheria* and *Eoleptestheria* are spherical and smooth with no clearly distinct differences (Fig. 14a-d). Species and genera of this family may be separated by adult characters only. The cyst pattern of several species of the Leptestheriidae – small with a smooth surface – has already been presented by BOTNARIUC (1947, Pl. I, Fig. 7: *Leptestheria intermedia*), THIÉRY (1987, 1995: *Leptestheria mayeti*), TOMMASINI & SCANABISSI SABELLI (1989, Figs 11, 12: *Leptestheria dahalacensis*), and BRENDONCK *et al.* (1993: *Leptestheria aegyptiaca*).

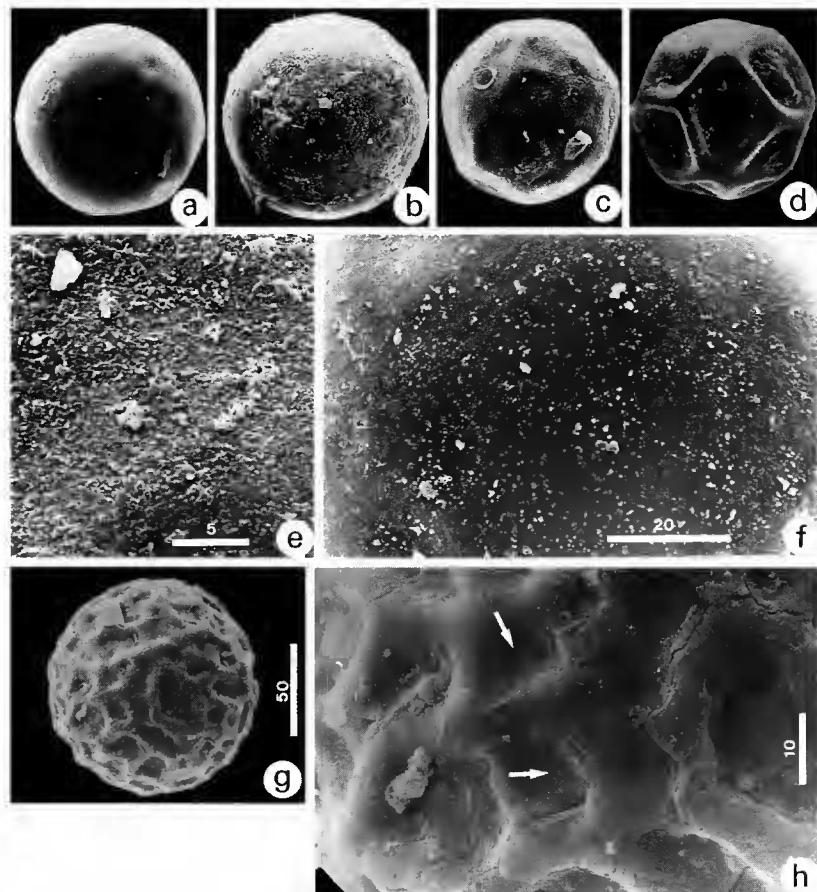


FIG. 14. — Cysts of conchostracans (Spinicaudata and Laevicaudata): a-c) *Leptestheria dahalacensis*; d) *idem*, not fully mature cyst deformed by preparation for scanning; e) *idem*, surface; f) detail of surface, *Eoleptestheria tictinensis*; g) *Lynceus brachyurus*; h) same species, detail of the surface showing depressions (arrows). (a-d), g): same scale.) (Scale bars in  $\mu\text{m}$ .)

*Oeufs de conchostracés (Spinicaudata et Laevicaudata) : a-c) Leptestheria dahalacensis ; d) idem, œuf immature déformé par la préparation pour le scanning ; e) idem, surface ; f) détail de la surface chez Eoleptestheria tictinensis ; g) Lynceus brachyurus ; h) même espèce, détail des dépressions de surface (flèches). (a-d), g) : même échelle.) (Échelles en  $\mu\text{m}$ .)*

LIMNADIIDAE (Fig. 13): cysts of *Limnadia* and *Innadia* are now well known (THIÉRY & GASC, 1991). The present material supplies additional pictures but no new information. In *Limnadia*, the cyst is clam-shell like and biconcave with ridges converging to an apical point (Fig. 13a-c), so that MARTIN (1989) called them “twisted eggs”. No objective difference could be observed between the cysts of American populations described by MARTIN (1989) and those of European populations described by SARS (1896), DADAY (1925), ZAFFAGNINI (1967), and THIÉRY & GASC (1991).

*Innadia* cysts have a spiral aspect (Fig. 13d, e), as illustrated by BOTNARIUC (1947), BTREK (1957, Fig. 2h), and THIÉRY & GASC (1991). In both *Limnadia* and *Innadia* the cyst patterns are unique in the “large branchiopods” and can be considered as generic.

LAEVICAUDATA (Fig. 14): cysts of *Lynceus brachyurus* are spherical and look like a small golf-ball with more or less angular depressions (Fig. 14g, h). They are among the smaller cysts of European phyllopods (approximately 120 µm). Cysts of *Lynceus andronachensis* illustrated by BOTNARIUC (1947, Pl. I, Fig. 15) resembles those of *L. brachyurus*.

## DISCUSSION

From our observations, complemented by reliable data in the literature, it appears that the species present a relatively constant morphology of the mature cysts over their whole distributional area. However, the fact that the surface pattern and size sometimes presents relative variability is hardly discussed by MURA (1991a, 1992a, b). In the case of phyllopods it is true that several species, occupying a large distribution area, present more or less important differences in size between populations of different habitats particularly between those in lowlands and high mountains (THIÉRY, 1987, in prep.; BELK *et al.*, 1990; MURA, 1991b). In these cases the size is statistically different but the external pattern remains quite similar.

When species have cysts with similar surface patterns, their size usually allows their identification. When the two characters are unable to allow a clear distinction, it is useful to consider the structure of the shell, as in the case of *Artemia* and *Branchinectella media* (spongy vs roots/pillars). Only a small number of species have markedly similar cysts (*Leptestheria* and *Eoleptes-theria* in the Leptestheriidae, *Branchinecta paludosa* and *B. ferox*, the different species of the genus *Tanymastix*, and several notostracans). In the case of *Branchinecta orientalis* and *B. minuta*, the fact that the cysts closely resemble each other in pattern and size raises the question of an eventual synonymy, as was the case for *Branchipus blanchardi* and *B. alpinus* (see the respective cysts in MURA, 1986, Pl. 13b, and THIÉRY & GASC, 1991, Figs 16, 28).

For about 80% of the European species, the combination of surface pattern/size is a valid means of species identification. In some other cases, *e.g.* *Tanymastix*, *Branchipus*, *Cyzicus*, cyst morphology presents only a generic peculiarity.

As observed in most of species of Anostraca (HELLSTRÖM & NAUWERCK, 1971; THIÉRY, 1987), the number of resting eggs is related to the length of the female. Except some cases (BELK *et al.*, 1990), the size of cysts is usually approximately constant from the first to last batches (BELK, 1977; MURA, 1991b). Considering the absolute value of the size of the cysts within the Anostraca, Notostraca, Spinicaudata and Laevicaudata, our study allows us to

distinguish three groups: notostracans with eggs larger than 450 µm, conchostracans with eggs less than 200 µm, and, between these groups anostracans with cysts from 250 to 450 µm. This is in accord with the gradient found by THIÉRY (1987) for Moroccan "large brachiopods", by THIÉRY & GASC (1991) for French species, and by BRENDACK *et al.* (1993) for tropical African species.

Our study needs, however, to be completed by the description of cysts of species which are lacking in this paper (lack of material such as *Chirocephalus ripophilus*, *C. robustus*, *C. reiseri*, *C. horribilis*, or immature cysts such as in the case of *Drepanosurus birostratus*). Also, even though egg morphology seems to be a useful species- or genus-specific character, the full extent of its taxonomic value in some cases remains limited. Some cysts of different species are very similar. Despite cases which are the subject of conflicting opinions, cyst morphology, shape, and size taken together often represent a useful adjunct to identification which should be included along with classical species descriptions, as was done for example by MAEDA-MARTINEZ *et al.* (1992, 1993), and SMITH (1992). However, the choice of cysts (maturity level) and measurements need stringent attention, to avoid the confusions or errors (erroneous scale bars) which cause some data to be unusable. (Errors and omissions found in all references about cysts are noted in Table I).

Cyst data also provide additional support for the close relationship recognized between certain anostracans on other grounds by DADAY (1910). For example, in the Chirocephalidae, if the cyst morphology pattern of different species follows in part the groups determined on classical characters of the male (antennae, penes), it is sometimes discordant (e.g. the heterogenous *Pristiccephalus*-group). In consequence it will be interesting to study large series of cysts from different populations to prove or disprove statistically that the size of cysts is more or less constant and not correlated with the length/age of the female. It will be also useful to consider whether size is linked with altitude, as in *Triops cancriformis* and *Chirocephalus diaphanus* in Morocco (THIÉRY, 1987), or in *Chirocephalus* in Italy (MURA, 1991b).

Finally, the morphological study of cysts has reached its limits and needs to be completed by biochemical studies which may provide insights into the formation of so great a variety of egg shells in the "large brachiopods" (spiny, bumpy, lenticular, spiral, twisted, smooth, etc.). Research dealing with this subject, previously discussed by THIÉRY (1987, p. 338), is in progress. We think also that isoelectric focusing data could help to clarify the taxonomy of several families, the Chirocephalids for example. This technique could also measure the genetic distance between the five endemic species of *Branchipus*, the genetic distance between the Linderiellidae and Chirocephalidae, between *Leptestheria* and *Eoleptestheria*, and help determine a hierarchy in characters (importance of the cyst vs penes, or antennae). We will use biochemical methods which were initiated in anostracan studies by SIEDEL & SIMPSON (1984), NAVARRO *et al.* (1987), REQUINTINA & SIMPSON (1987), FUGATE (1992), THIÉRY & FUGATE (1994), for more extensive research.

#### Acknowledgements

We thank Dr G. FRYER for the loan of specimens of *Lepidurus arcticus* from Iceland, Dr N. A. AKATOVA (Saint Petersburg), Pr G. MURA (Roma), Dr S. PETKOSVKI (Skopje), and Dr N. VEKHOFF (Moscow), for several preserved anostracans, and Dr D. DEFAYE (MNHN Paris) for access to the Muséum collections. The first author thanks Dr D. BELK and Pr H. J. DUMONT for their useful remarks.

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TABLE 1. — Recapitulative list of cyst measurements of European "phyllopods". Species cited in the checklist of BRTEK & THIÉRY (1995) which are not in this table have cysts which remain unknown. n = number of measured cysts, V. I. = variation index, S = standard error,  $\bar{x}$  = mean. The symbol ?? in the column of measurements indicates that the value is doubtful, corresponding most of the time to a scale-bar error.

Liste récapitulative des mesures des œufs des espèces de « phyllopodes » actuellement connues en Europe. Les œufs des espèces citées dans la liste de BRTEK & THIÉRY (1995) qui ne sont pas dans ce tableau ne sont pas connus. n = nombre d'œufs mesurés, V. I. = indice de variation (en %),  $\bar{x}$  = moyenne, S = erreur standard. Le symbole ?? dans la colonne des mesures indique que la valeur tirée d'une référence bibliographique est douteuse, la plupart du temps suite à une erreur d'échelle.

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n = )]	REFERENCE IN LITERATURE	LOCALITY
<b>ANOSTRACA</b>			
<i>Polyartemia forcipata</i> (V. I. = 15.76 %)	527 µm (n = 1)  0.45 mm	This study  HELLSTRÖM & NAUWERCK (1971)	Russia  Sweden
<i>Branchinecta ferox</i> (V. I. = 24.61 %)	386 - 412 µm (n = 6)  352 - 383 µm (n = 3)  0.36 - 0.42 mm  error in scale  438 µm  342 µm  0.241 mm (cysts clearly immature)	This study  This study  ALONSO (1985)  ALONSO & ALCARAZ (1984)  MURA & THIÉRY (1986)  PETKOVSKI (1991b)  CÉSAR (1989)	Slovakia  Slovakia  Spain  Spain  Morocco  Yugoslavia  MHN Paris without reference
<i>Branchinecta minuta</i>	290 - 305 µm (n = 3)	This study	Russia

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n = )]	REFERENCE IN LITERATURE	LOCALITY
<i>Branchinecta orientalis</i> (V. I. = 37.40 %)	277 - 280 µm (n = 2)	This study	Austria
	219 µm	ALONSO & ALCARAZ (1984)	Spain
	0.22 - 0.32 mm	ALONSO (1985)	Spain
	263 µm	PETKOVSKI (1991b)	Yugoslavia
<i>Branchinecta paludososa</i> (V. I. = 47.64%)	394 - 442 µm (n = 3)	This study	Slovakia
	264 µm /?	MURA (1991a)	North America
	320 - 325 µm (n = 15)	This study	Russia
	0.396 mm	CÉSAR (1989)	MNHN Paris without reference
	0.27 - 0.38 mm ( $\bar{x}$ = 0.35 mm, n > 30)	BELK (1977)	USA-Arizona
<i>Branchinecta tolli</i> (V. I. = 7.43 %)	311 - 335 µm (n = 7)	This study	Russia
<i>Artemia parthenogenetica</i> (V. I. = 27.51 %)	216 - 269 µm [ $\bar{x}$ = 240.3 µm, SD = 18.43, n = 10]	This study	France
	220 - 270 µm	THIÉRY & GASC (1991)	France
	241.2 µm	VIDELA & CASTELA BRANCO (1987)	Portugal
	259 µm	VANHAECKE & SORGELOOS (1980)	France
	266 µm (n = 50)	VIEIRA & AMAT (1985)	Portugal
	238.8 µm	THIÉRY & ROBERT (1992)	France
	251.8 - 263.1 µm	CASTRITSI - CATHARIOS <i>et al.</i> (1987)	Greece
	260.1 - 264.7 µm (n = 500)	ABATZOPoulos <i>et al.</i> (1987)	Greece
	270.1 - 279.3 µm (in laboratory culture)	ABATZOPoulos <i>et al.</i> (1987)	Greece
	208 - 234 µm (n = 14)	THIÉRY (in press)	Saudi Arabia
	15.3 - 28.9 µm /? ( $\bar{x}$ = 24.1 µm)	MAJIC & VUKADIN (1987)	Yugoslavia
	259.6 µm	VANHAECKE & SORGELOOS (1980)	France (Aigues-Mortes)
	276.3 µm	VANHAECKE & SORGELOOS (1980)	France (Lavalduc)
	264.4 µm	VANHAECKE & SORGELOOS (1980)	France (Salins de Giraud)
	257.8 µm	VANHAECKE & SORGELOOS (1980)	France (Salins d'Hyères)
	253.6 µm	VANHAECKE & SORGELOOS (1980)	Spain
	284.9 µm	VANHAECKE & SORGELOOS (1980)	Italy

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n = )]	REFERENCE IN LITERATURE	LOCALITY
<i>Artemia tunisiana</i> (bisexual) (V. I. = 31.57 %)	0.20 - 0.25 mm	MATHIAS (1937)	France
	255.39 µm (n = 655)	TRIANTAPHYLLOIDES <i>et al.</i> (1993)	Greece Lesbos Island-Kallon
	269.71 µm (n = 777)	TRIANTAPHYLLOIDES <i>et al.</i> (1993)	Greece Lesbos Polychnitos
	208 - 286 µm (n = 5)	This study	France (Sète)
	231.2 - 268.0 µm	VIDELA & CASTELA BRANCO (1987)	Portugal
	245 µm	Thiéry & Gasc (1991)	France (Sète)
	245.3 µm	Thiéry & Robert (1992)	France (Sète)
	222-234 µm (probably a New World bisexual strain-not <i>A. tunisiana</i> )	MAILLARD & BAUDET (1980)	France (Guérande)
	288 - 290 µm (n = 3)	This study	France (Alps-Cristol plateau)
	300 µm	THIÉRY & GASC (1991)	France (Alps-Cristol plateau)
<i>Branchipus blanchardi</i> (V. I. = 19.18 %)	# 0.35 mm	ALONSO (1989)	France (Alps)
	291 µm	MURA (1986)	Italy (Alps)
	0.25 mm	ALONSO & JAUME (1991)	Spain
	200 µm	ORGHIDAN (1947)	Romania
	228 - 270 µm (n = 5)	This study	France (Languedoc)
	205 - 250 µm (n = 4)	This study	France (Crau)
	238 - 253 µm (n = 4) syn. <i>visnyai</i>	This study	Slovakia
	254 µm - syn. <i>visnyai</i>	MURA (1986)	Italy
	195 µm	KUPKA (1940)	not indicated
	0.25 mm	GILCHRIST (1978)	not indicated
<i>Branchipus cortesi</i> <i>Branchipus intermedius</i> <i>Branchipus schaefferi</i> (V. I. = 42.36 %)	0.2 - 0.3 mm	ALONSO (1985)	Spain
	0.2 - 0.28 mm	MATHIAS (1937)	not indicated
	320 µm /?	MURA (1986)	Italy
	253 µm	MURA & THIÉRY (1986)	Morocco
	260 - 289 µm (n = 10)	THIÉRY (1995)	Saudi Arabia
	0.35 mm	PETKOVSKI (1995)	Macedonia
	300/313 - 192/195 µm (n = 5)	This study	France
	0.233 / 0.164 mm	GARREAU DE LOUBRESSE (1982)	France
	337.8 µm	ALONSO & ALCARAZ (1984)	Spain
	0.40 - 0.43 mm	ALONSO (1985)	Spain

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n = )]	REFERENCE IN LITERATURE	LOCALITY
<i>Tanymastix stellae</i>	0.43 mm	AL-TIKRITY & GRAINGER (1990)	Ireland
	0.35 - 0.40 mm	PETKOVSKI (1995)	Macedonia
	370 µm	CHAMPEAU & THIÉRY (1990)	Corsica
<i>Branchinella spinosa</i> (V. I. = 15.35 %)	485 µm ?/	MURA (1986)	Sardinia
	250 - 260 µm	MURA (1992b)	Italy
	260.1 µm	THIÉRY & GASC (1991)	France (Camargue)
	223 µm	MURA & THIÉRY (1986)	Morocco
	224 µm	MURA (1986)	Italy
	225 - 235 µm	THIÉRY (in press)	Saudi Arabia
<i>Streptocephalus torvicornis torvicornis</i> (V. I. = 42.76 %)	263 - 279 µm (n = 3)	This study	Slovakia
	0.3 mm	VALOUSEK (1952)	Czechoslovakia
	0.22 - 0.33 mm	ALONSO (1985)	Spain
	250 µm	ALONSO & ALCARAZ (1984)	Spain
	240 µm	MURA (1992a)	Origin not indicated
	231 - 239 µm (n = 8)	THIÉRY (1995)	Saudi Arabia
<i>Streptocephalus torvicornis buchetii</i> (V. I. = 12.29 %)	0.22 mm	ZOGRAF (1907)	Russia
	244.3 µm	ALONSO & ALCARAZ (1984)	Spain
	276.3 µm	MURA & THIÉRY (1986)	Morocco
	240 - 260 µm	THIÉRY & GASC (1991)	France
	0.23 - 0.26 mm	ALONSO (1985)	Spain
	255 µm	ALONSO & ALCARAZ (1984)	Spain
<i>Chirocephalus brevipalpis</i>	(316 µm from fig.1.e, but the text indicates 0.22 - 0.24 mm)	PETKOVSKI (1991a)	Yugoslavia
	(erroneous scale bar in the figure, Petkovski, ab ora)		
<i>Chirocephalus carnuntanus</i>	240 - 260 µm (n = 4)	This study	Slovakia
<i>Chirocephalus chyzeri</i>	0.154 mm (immature cyst)	ZOGRAF (1907)	not indicated
<i>Chirocephalus diaphanus</i>	259 - 310 µm (n = 5)	This study	Slovakia
(V. I. = 52.08 %)	370 - 429 µm (n = 6)	This study	Slovakia
	360 - 420 µm	THIÉRY & GASC (1991)	France
	340 µm	ALONSO & ALCARAZ (1984)	Spain

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n = )]	REFERENCE IN LITERATURE	LOCALITY
	287 µm	MURA <i>et al.</i> (1978)	Italy
	0.25 - 0.32 mm	ALONSO (1985)	Spain
	0.43 mm	HALL & MAC DONALD (1975)	England
	270 µm	POISSON <i>et al.</i> (1946)	France
	0.25 mm	MATHIAS (1937)	not indicated
	error in scale	MURA (1992b)	Italy
<i>Chirocephalus diaphanus carinatus</i>	270 - 288 µm (n = 9)	This study	Bulgaria
<i>Chirocephalus josephi-nae</i>	331 - 345 µm (n = 3)	This study	Russia
<i>Chirocephalus kerky-rensis</i> (V. I. = 21.48 %)	0.25 mm	ZOGRAF (1907)	Russia
	266 - 331 µm	MURA (1986)	Italy
	error in scale	MURA (1992b)	Italy
	311 µm (n = 50)	MURA <i>et al.</i> (1978)	Italy
<i>Chirocephalus marchessonii</i>	428 µm (n = 50)	MURA <i>et al.</i> (1978)	Italy
	363 µm	MURA (1986)	Italy
	error in scale	MURA (1992b)	Italy
<i>Chirocephalus orgidani</i> (V. I. = 5.99 %)	275 - 292 µm (n = 3)	This study	Roumania
<i>Chirocephalus pelago-nicus</i> (V. I. = 12.10 %)	295 - 296 µm (n = 2)	This study	Yugoslavia
<i>Chirocephalus ruffoi</i>	333 µm	PETKOVSKI (1986)	Yugoslavia
	252 µm	MURA (1986)	Italy
	no scale	COTTARELLI & MURA (1984)	Italy
	error in scale	MURA (1992b)	Italy
<i>Chirocephalus salinus</i>	345 - 363 µm (n = 4)	This study	Corsica
	341 - 360 µm (n = 4)	THIÉRY & GASC (1991)	Corsica
	355 µm	CHAMPEAU & THIÉRY (1990)	Corsica
	256 µm ??	MURA <i>et al.</i> (1978)	Sardinia
	362 µm	MURA (1986)	Sardinia (code 600)
	256 µm ??	MURA (1986)	Sardinia (code 300)
	error in scale	MURA (1992b)	not indicated
<i>Chirocephalus shadini</i>	275 - 280 µm (n = 6)	This study	Slovakia
<i>Chirocephalus slovac-cus</i> (V. I. = 10.52 %)	311 - 325 µm (n = 3)	This study	Slovakia
	306 - 332 µm (n = 5)	This study	Slovakia
	329 - 340 µm (n = 3)	This study	Slovakia

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n = )]	REFERENCE IN LITERATURE	LOCALITY
<i>Chirocephalus spini-caudatus</i>	264 µm	This study	France (MNHN Paris Bp. 157)
<i>Chirocephalus sibyllae</i>	290 µm error in scale	MURA (1986) MURA (1992b)	Italy Italy
<i>Drepanosurus birostaurus</i>	173 µm, but immature cyst	This study	Russia
<i>Drepanosurus hankoi</i>	341 - 358 µm (n = 5) 300 µm	This study MURA (1992b)	Slovakia origin not indicated
<i>Siphonophanes grubii</i> (V. I. = 16.23 %)	353 µm (n = 1) 0.30 - 0.33 mm 312 µm	This study BUCHHOLZ (1864) MURA (1992b)	Slovakia (MNHN Paris Bp. 260) Germany not indicated
<i>Branchinectella media</i> (V. I. = 6.36 %)	198 - 211 µm (n = 3) 208.6 µm 0.2 mm	This study Alonso & Alcaraz (1984) ALONSO (1985)	Russia Spain Spain
<b>NOTOSTRACA</b>			
<i>Lepidurus apus</i> (V. I. = 26.08 %)	436 - 485 µm (n = 5) 432 - 495 µm (n = 12) 455 - 471 µm (n = 4) 496 µm (n = 1) 0.4 - 0.5 mm 479 µm 0.6 mm 440 µm 0.4 - 0.6 mm 430 - 520 µm	This study This study This study This study ALONSO (1985) ALONSO & ALCARAZ (1984) RÉAU DE LA GAINNONNIÈRE (du) (1908) ARNOULT (1951) MATHIAS (1937) THIÉRY & GASC (1991)	France (Provence) - dried South-France (Gavot) France (Languedoc) Slovakia Spain Spain France (Angers) France (Toulouse) not indicated France Mongolia Russia not indicated
<i>Lepidurus couesii</i>	420 - 425 µm (n = 3)	This study	
<i>Lepidurus arcticus</i> (V. I. = 14.78 %)	603 - 621 µm (n = 3) 0.7 mm 700 µm	This study BRAEM (1893) FRYER (1988)	
<i>Triops cancriformis</i> (V. I. = 16.21 %)	350 - 380 µm (n = 3) 368 - 372 µm (n = 6) 355 - 375 µm (n = 4) 0.37 mm 360 - 400 µm 0.4 - 0.6 mm /?/ 0.34 mm	This study This study This study GILCHRIST (1978) THIÉRY & GASC (1991) MATHIAS (1937) TOMMASINI <i>et al.</i> (1989)	Slovakia France (Opoul) France (Crau) England France (Languedoc) France Italy

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n = )]	REFERENCE IN LITERATURE	LOCALITY
<i>Triops Cancriformis mauritanicus</i>	423 µm	ALONSO & ALCARAZ (1984)	Spain
(V. I. = 18,98 %)	442 - 510 µm	THIÉRY (1987)	Morocco
<i>Triops Cancriformis simplex</i>	391 µm	ALONSO & ALCARAZ (1984)	Spain
(V. I. = 5,52 %)	370 µm	THIÉRY (1987)	Morocco
<i>Triops numidicus</i>	1 mm	GHIGI (1921)	not indicated
	625 - 750 µm	THIÉRY (1987)	Morocco
<b>SPINICAUDATA</b>			
<i>Limnadia lenticularis</i>	185 - 209 µm (n = 2)	This study	Slovakia
(V. I. = 12,18 %)	199 - 208 µm (n = 2)	This study	Slovakia
	200 - 208 µm	THIÉRY & GASC (1991)	not indicated
	0,15 - 0,22 mm	LEREBOULLET (1866)	not indicated
	0,15 - 0,17 mm	ZAFFAGNINI (1967)	Italy
<i>Imnadia yeyetta</i>	180/180 - 185/190 µm (n = 2)	This study	Slovakia
(V. I. = 11,23 %)	165/150 - 175/160 µm (n = 6)	This study	France (Crau)
	185/182 µm	THIÉRY & GASC (1991)	not indicated
<i>Cyzicus tetracerus</i>	146 - 161 µm (n = 7)	This study	Slovakia
(V. I. = 14,30 %)	141 - 153 µm (n = 5)	This study	Slovakia
	145 - 150 µm	THIÉRY & GASC (1991)	France (Provence)
	139,5 µm	ALONSO & ALCARAZ (1984)	Spain
	0,15 - 0,16 mm	MATHIAS (1937)	France
<i>Cyzicus grubei</i>	124 µm	ALONSO & ALCARAZ (1984)	Spain
<i>Cyzicus buchetii</i>	150 - 190 µm	THIÉRY (1987)	Morocco
<i>Eocyzicus orientalis</i>	119 - 122 µm (n = 2)	This study	Russia
(V. I. = 2,49 %)			
<i>Leptestheria dahalicensis</i>	95 - 103 µm (n = 3)	This study	Slovakia
(V. I. = 14,63 %)	103 - 110 µm (n = 8)	This study	Slovakia
	100 µm	SCANABISSI SABELLI & TOMMASINI (1992)	Italy
<i>Leptestheria mayeti</i>	179 µm	THIÉRY (1987)	Morocco
<i>Eoleptestheria ticinensis</i>	125 - 130 µm (n = 5)	This study	Slovakia
(V. I. = 6,35 %)	122 - 126 µm (n = 4)	This study	Slovakia
	127 µm	THIÉRY & GASC (1991)	France (Camargue)
<b>LAEVICAUDATA</b>			
<i>Lynceus brachyurus</i>	114 - 119 µm (n = 2)	This study	Slovakia
(V. I. = 4,29 %)			